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# Information Feedback from Photophores and Ventral Countershading in Mid-Water Squid[1]

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ABSTRACT: The arrangement of photosensitive vesicles and photophores in two species of mid-water squid suggests that the vesicles function in detecting the intensity of downward-directed surface light and the intensity of light from their own photophores. This information is precisely what is required for an animal to eliminate its ventral shadow by the production of a ventral bioluminescent glow. This arrangement, therefore, offers strong support for the theory of ventral countershading in mid-water animals.

Cephalopods have photoreceptive structures other than the eyes. In octopods these organs have been called epistellar bodies (Young, 1929); in squid and cuttlefish they have been labeled the parolfactory vesicles (Boycott and Young, 1956). In both instances the names are associated with the location of the organs: in octopods, on the stellate ganglia; and in squid and cuttlefish, near the olfactory lobe on the optic stalk of the brain. In spite of the different locations of these organs, they are probably homologous structures (Nishioka, Hagadorn, and Bern, 1962; Nishioka et al., 1966, and personal observations). It is, therefore, no longer desirable to maintain a separate terminology in the different groups. Since neither of the present names is appropriate to all cephalopod groups, it becomes necessary to rename the organs. Since these organs are photoreceptors (Nishioka et al., 1966; Mauro and Baumann, 1968; Mauro and Sten-Knudsen, 1972), it is suggested that the epistellar bodies and the parolfactory vesicles be called the photosensitive vesicles.[3]

The function of the photosensitive vesicles beyond their photosensitive capacity is unknown. One probable function, however, has recently emerged during the course of a study which is attempting to correlate modifications of the photosensitive vesicles with certain aspects of the ecology of mid-water cephalopods off Hawaii.

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## RESULTS

Pelagic cephalopods living below the epipelagic zone during the daytime (i.e., in the mid-water environment) have photosensitive vesicles which exhibit many variations; these often involve hypertrophy of the organs. Two such variations have already been reported (Messenger, 1967; Baumann et al., 1970). The most striking modifications that I have observed occur in some members of the squid family Enoploteuthidae. Although the arrangement varies somewhat between the species examined, most basic elements of the general pattern remain constant. The animals studied in most

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[3] An abstract, treating the modifications of the photosensitive vesicles in mid-water squid, was published in the Proceedings of the Joint Oceanographic Assembly, Tokyo, 1971. In this abstract I used the term "photic vesicles." J. Z. Young has since informed me that this term had already been used for certain light-sensitive structures in gastropods. Following his suggestion, I now adopt the term "photosensitive vesicles."

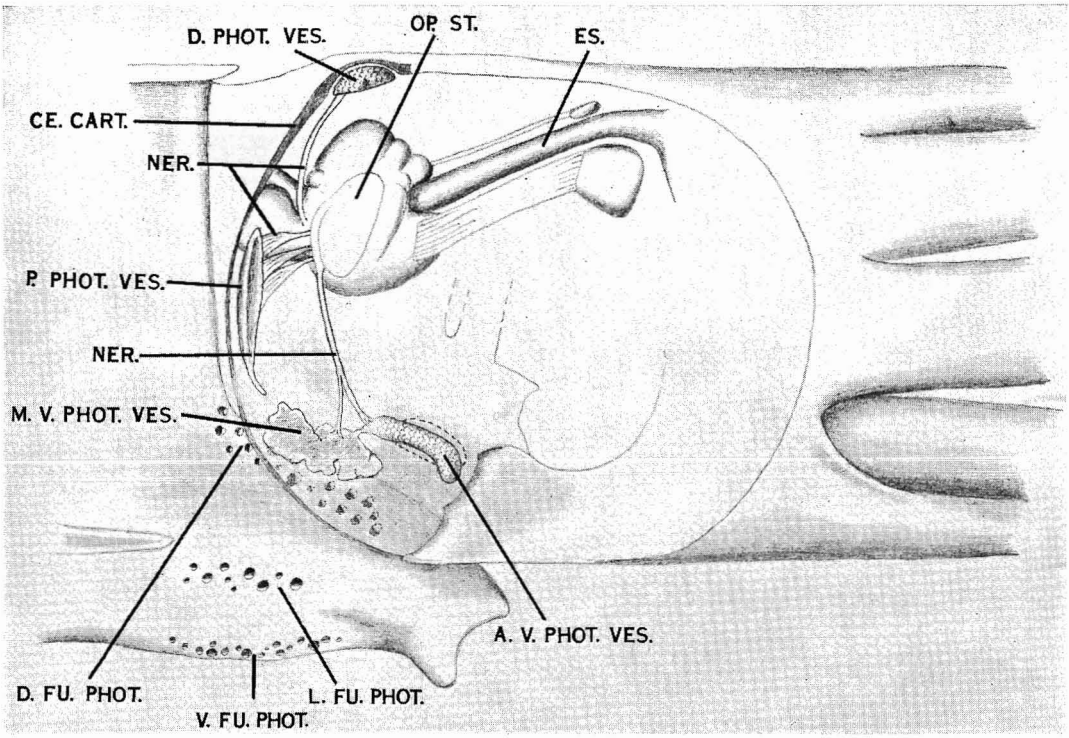


FIG. 1. Lateral dissection of the head of *Abraliopsis* sp.

SYMBOLS: A. V. PHOT. VES., anterior ventral photosensitive vesicles; CE. CART., cephalic cartilage; D. FU. PHOT., dorsal funnel photophores; D. PHOT. VES., dorsal photosensitive vesicles; L. FU. PHOT., lateral funnel photophores; M. V. PHOT. VES., mid-ventral photosensitive vesicles; NER., nerve; OP. ST., optic stalk; P. PHOT. VES., posterior photosensitive vesicles; V. FU. PHOT., ventral funnel photophores.

detail belong to two undescribed species of *Abraliopsis* (Burgess, in manuscript). Both of these species are commonly captured in mid-water trawls off Hawaii. Although the data are rather sparse, these species seem to occupy depths during the daytime around 600 meters and at night they migrate into the upper hundred meters.

The structure and arrangement of the photosensitive vesicles in these species of *Abraliopsis* differ greatly from those found in neritic or epipelagic squid. The unusual arrangement of vesicles is described in the following paragraphs and provides the basis for the subsequent discussion.

Squid occupying near-surface waters generally have a single, small set of vesicles. In contrast, these deeper living species of *Abraliopsis* have three to four greatly enlarged sets, all well removed from the usual position on the optic stalks of the brain. All of the vesicles lie within the head adjacent to the inner wall of the cephalic cartilage. One set is situated dorsally; two are ventrally located; and the fourth, which is absent in one species, occupies a posterior position within the head (Fig. 1). Each member, or lobe, of a set consists of a number of individual vesicles, each with a lining of cell bodies that have photosensitive processes extending into a central lumen.

Each lobe of the dorsal set of vesicles lies close to the dorsal surface of the head and protrudes into a concavity in the cephalic cartilage. As a result, the cartilage above each lobe is very thin. Muscle tissue, although present on all surrounding areas, is absent from most of the area immediately above the dorsal vesicles. Therefore, between the vesicles and the surface lie only the thin cephalic cartilage and the integument. The integument over most of the surface

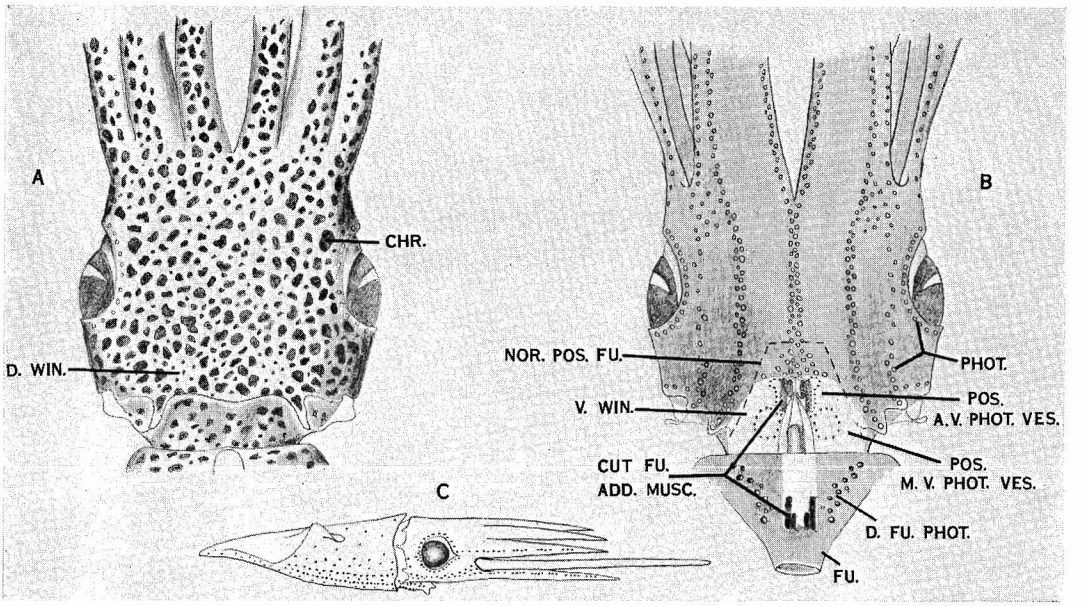


FIG. 2. *A*, dorsal view of head of *Abraliopsis* sp. *B*, ventral view of head of *Abraliopsis* sp. with the funnel adductor muscles cut and the funnel reflected posteriorly. Shaded portion indicates areas covered by chromatophores. *C*, lateral view of *Abraliopsis* sp. showing ventral predominance of photophores.

SYMBOLS: CHR., chromatophore; CUT. FU ADD. MUSC., cut funnel adductor muscle; D. FU. PHOT., dorsal funnel photophores; D. WIN., dorsal window; FU., funnel; NOR. POS. FU., normal position of the funnel; PHOT., photophores; POS. A. V. PHOT. VES., position of the anterior ventral photosensitive vesicles; POS. M. V. PHOT. VES., position of the mid-ventral photosensitive vesicles; V. WIN., ventral window.

of the head contains two layers of chromatophores. The innermost layer is absent from the integument immediately above the vesicles and the other layer is usually observed with all chromatophores contracted. This arrangement provides a distinctive "window" on the surface of the head through which light has easy access to the dorsal vesicles (Fig. 2*A*). Viewed dorsally, each lobe has a nearly circular shape except for a V-shaped indentation on its lateral margin. The dorsal surface of the lobe is smooth and convex while the ventral surface is approximately flat but rather irregular.

Each dorsal lobe appears to consist of a single layer of elongate vesicles oriented perpendicular to the dorsal surface of the lobe. The cross sections of individual vesicles are approximately circular. Cell bodies of the photosensitive cells are found primarily along the sides and dorsal ends of the individual vesicles, and the photosensitive processes, in general, are aligned with the long axis of each vesicle. Large flattened bundles of nerves from each dorsal lobe extend ventrally along the inner surface of the cephalic cartilage and enter the brain in the region of the peduncle lobe.

The ventral sets of vesicles are shaped quite differently from the dorsal one. The most anterior of the two ventral sets consists of somewhat flattened, sausage-shaped structures with thickened and laterally curved anterior ends (Fig. 1). Each lobe of this anteroventral set lies in a depression in the floor of the cartilage except for a small medial projection which partially lies in a foramen in the cartilage. Each lobe seems to consist of a single layer of vesicles. At the thickened anterior end, the vesicles are elongate and have their long axes approximately perpendicular to the convex ventral surface of the organ. The flatter, posterior portions of each lobe have somewhat irregular elongate vesicles which lie parallel to the ventral surface of the organ. Cell bodies of the photosensitive cells occur in a compact layer on all surfaces of the individual vesicles but predominate on the side and ventral margins of the vesicles. Each

anteroventral lobe is in contact with another lobe, the mid-ventral lobe, via a narrow strand of vesicles.

In contrast to the anteroventral lobes, the mid-ventral lobes are very irregular in outline and are extraordinarily thin (Fig. 1). Individual vesicles are short and irregular in shape and lack apparent orientation. Cell bodies of the photosensitive cells predominate along the sides of the vesicles and are often absent from the flattened dorsal and ventral surfaces.

A large nerve passes from the ventral sets of vesicles along the inner wall of the cephalic cartilage to the region of the peduncle lobe of the brain.

The surface of the head immediately below the vesicles has a distinctive appearance. This area, which also overlies the funnel, lacks chromatophores and photophores. Head retractor muscles which cover much of this area are transparent in the living animal. The ventral portion of the head between the ventral sets of vesicles and the funnel, therefore, forms an extensive ventral window through which light may reach the photosensitive vesicles (Fig. 2*B*).

The final pair of lobes, the posterior photosensitive vesicles, lies between the optic lobes of the brain and the posterior wall of the cephalic cartilage (Fig. 1). Each is elliptical in outline except in the extreme ventral portion where it tapers toward the mid-ventral vesicles with which it may or may not connect. The posterior lobes, in contrast to the colorless condition (when preserved) of the other lobes, have a distinctive yellow coloration in preserved (alcohol) specimens. Often several vesicles of the mid-ventral lobes which are nearest the posterior lobes exhibit this same yellow pigmentation. Each posterior organ is thin but thicker and more turgid than the mid-ventral lobes. The elongate vesicles of the posterior lobes are regularly aligned and oriented parallel to the ventral surface of the animal, i.e., they extend from the median margin toward the lateral margin of each organ; some vesicles traverse the entire width of a lobe. Cell bodies of photosensitive cells can be found, equally concentrated, around the entire circumference of the individual vesicles. Nerves appear to run in several flattened bundles from the posterior vesicles to a point in the brain near the peduncle lobe.

In order to interpret the probable functions of the dorsal and ventral sets of vesicles, it is necessary to examine the arrangements of photophores in these squid. These species of *Abraliopsis* possess numerous photophores over the surfaces of the body, head, and arms. As with many mid-water animals, the photophores are most abundant on the ventral surfaces and only a few scattered organs are present dorsally (Fig. 2*C*). The photophores are very complex, containing pigment screens, reflecting devices, and lenses. The photophores on the ventral half of the animal are oriented with lenses directed ventrally. Some of the photophores on the funnel provide a clear exception to this general arrangement.

The funnel bears six longitudinal series of photophores (Fig. 1). Two series are located on the ventral surface and each has 19 to 20 ventrally directed photophores. Another series is located on each ventrolateral portion of the funnel and has about 10 to 12 ventrally directed photophores. The final two series are located on the dorsal surface of the funnel, one on either side of the anterior funnel adductor muscles. Each of these series has 22 to 23 photophores which point in a general dorsal direction to a centrally located area on the ventral surface of the head. The most posterior of these photophores slant anteriorly and medially, whereas the most anterior ones slant medially only (Fig. 1). All of these photophores, therefore, are directed precisely toward the ventral sets of photosensitive vesicles. It appears that light passes from the dorsal funnel photophores through the "ventral window" to these vesicles. These squid appear to be monitoring light from their own photophores.

## DISCUSSION

Information feedback from these photophores in *Abraliopsis* could be useful in regulating the spectral composition of the light emitted or in regulating some type of flash pattern. It seems more likely, however, that the information is used in regulating the intensity of the bioluminescent light. Although there is no direct evidence that these species have this capacity, such an ability would be of great value.

These two species of *Abraliopsis* live in mesopelagic waters during the day where the penetration of surface light is probably of sufficient intensity to be detected by the highly sensitive eyes of many mid-water animals (Clarke and Denton, 1962). Clarke (1963) and Fraser (1962) have pointed out that animals living in this zone would be silhouetted against the downward-directed light and thereby become visible to predators below them. They have suggested that the predominantly ventral arrangement of photophores found in many animals living in this zone allows their possessor to produce a beam of downward-directed light which matches that from the surface and obliterates the silhouette. Nicol (1967) has discussed this hypothesis of ventral countershading at some length, and Denton (1970) has pointed out that the structure of the photophores and the pattern of emitted light in the hatchet fish, *Argyropelecus*, as well as the coloring of this fish, fit well with this hypothesis. Foxton (1970) has found that the distributional patterns of decapod crustaceans are compatible with this hypothesis. For countershading to be most effective it is probably necessary for bioluminescent light to be produced throughout the daylight period. It is possible, however, that intermittent countershading may be part of an escape mechanism which utilizes retreat rather than concealment through countershading. Unfortunately, there is no direct observational evidence that concerns this problem.

In order to utilize ventral countershading, a species might distribute along a specific isolume. Such a situation, however, would restrict a species to a narrow depth range due to the rapid change of light intensity with depth and would, presumably, necessitate frequent movement due to short-term fluctuations in light intensity. Alternatively, ventral countershading would be feasible if the animals could determine the intensity of downward-penetrating surface light and could regulate the luminous output of their photophores to match this light.

*Abraliopsis* probably orients in the water with its longitudinal body axis in a horizontal position. This is the typical attitude for squid in the families Loliginidae, Ommastrephidae, and probably others. I have observed the closely related enoploteuthid, *Abralia veranyi*, swimming in this position around a night light near the Bahama Islands. In this position, the dorsal photosensitive vesicles would be well situated for the detection of downward-directed surface light. The ventral vesicles are ideally suited for detecting the intensity of light from the animal's own photophores. The necessary sensory mechanism which would allow ventral countershading, therefore, is present.

This mechanism may have an analogous counterpart in certain mid-water fishes. Stomiatoid fishes have photophores that are directed into the eyes (Marshall, 1954). Many explanations have been proposed for this peculiar arrangement. Pütter (1902) thought that this light would produce a subliminal illumination of the retina, thereby lowering the effective visual threshold. Brauer (1908) considered that this light might make it easier for a species to recognize the distinctive quality of its own light, thereby facilitating recognition of conspecific individuals. Marshall (1954, 1966) suggested that the light might sensitize the retina prior to turning on the strong body photophores. Nicol (1967) wondered if these photophores might permit the fish to compare luminous output with the light of the environment or that they might enable a fish to signal by clocking its emission against a response from another fish. Both Brauer and Nicol, therefore, have suggested that these fish have a system of bioluminescent feedback. The analogous (and more clear-cut) situation in *Abraliopsis* supports this general interpretation.

If ventral countershading does occur, it is almost certainly not the sole function of these photophores, as each species exhibits a distinctive photophore arrangement which suggests a species-recognition function. Nor can ventral countershading be the only reason for the ventral predominance of photophores. Foxton (1970) pointed out that some species of *Sergestes* (*Sergia*) possess ventral photophores but occupy levels (below 700 m off the Canary Islands) at which the low light intensity would probably make countershading ineffective. This is also true for some deep living cephalopods (e.g., *Vampyroteuthis infernalis*, *Mastigoteuthis* spp.). In both sergestids and cephalopods the photophores found in the deepwater species are not as complex as those found in the shallower-

living species. Complex photophores (i.e., photophores with reflectors and lenses) are necessary for ventral countershading in order that most of the emitted light be collimated and directed vertically downward (Denton, 1970). If the light were not collimated to some degree, the portion of the expanding light beam beneath the animal would decrease in intensity much faster than the downward-penetrating surface light.

In conclusion, the ventral photosensitive vesicles in these species of *Abraliopsis* appear to detect bioluminescent light from the animal's own photophores while the dorsal vesicles are well situated to detect downward-penetrating surface light. This arrangement strongly suggests that a countershading mechanism is operating and lends considerable support to the countershading hypothesis.

SUMMARY

1. The arrangement and structure of the photosensitive vesicles of two species of *Abraliopsis* are described.
2. One set of vesicles is located near the dorsal surface of the head, a second near the ventral surface, and the third near the posterior surface. The surface of the head adjacent to the dorsal and ventral organs either lacks or has a reduced number of chromatophores and, thereby, forms "windows" for the passage of light.
3. The dorsal vesicles are well positioned to detect downward-penetrating surface light.
4. The ventral vesicles lie within the head immediately above the funnel and oppose a series of photophores located on the funnel and directed at the vesicles. It is suggested that the ventral vesicles provide a feedback mechanism for determining the intensity of photophore light.
5. These squid live in a region of low light intensity and possess numerous photophores, located on the ventral half of the animal, which are oriented in a ventral direction (with the exception of the photophores on the dorsal surface of the funnel).
6. It is suggested that the arrangement of photophores and photosensitive vesicles provides a mechanism which allows adjustment of photophore light intensity relative to the intensity of downward-penetrating light from the surface. A ventrally produced beam of bioluminescent light of the proper intensity would eliminate the animal's silhouette and thereby aid in concealment.

## LITERATURE CITED

BAUMANN, F., A. MAURO, R. MILECCHIA, S. NIGHTINGALE, and J. Z. YOUNG. 1970. The extra-ocular light receptors of the squids *Todarodes* and *Illex*. Brain Res. 21: 275–279.

BOYCOTT, B. B., and J. Z. YOUNG. 1956. The subpedunculate body and nerve and other organs associated with the optic tract of cephalopods, p. 76–105. *In*: Bertil Hanström: Zoological papers in honour of his sixty-fifth birthday. Zool. Inst., Lund.

BRAUER, A. 1908. Die Teifsee-Fische. 2 Anat. Teil. Wiss. Ergebn. 'Valdivia' 15: 1–266.

CLARKE, G. L., and E. J. DENTON. 1962. Light and animal life, p. 456–468. *In*: M. N. Hill [ed.] The sea. Vol. 1. John Wiley and Sons, Interscience, New York.

CLARKE, W. D. 1963. Function of bioluminescence in mesopelagic organisms. Nature, Lond. 198: 1244–1246.

DENTON, E. J. 1970. On the organization of reflecting surfaces in some marine animals. Phil. Trans., ser. B, 258: 286–313.

FOXTON, P. 1970. The vertical distribution of pelagic decapods (Crustacea: Natantia) collected on the SOND cruise 1965. J. Mar. Biol. Ass. U.K. 50: 939–960.

FRASER, J. 1962. Nature adrift. DuFour Editions, Chester Springs, Pa. 178 p.

MARSHALL, N. B. 1954. Aspects of deep sea biology. Hutchinson, London. 380 p.

———. 1966. The life of fishes. World Publishing Co., Cleveland. 402 p.

MAURO, A., and F. BAUMANN. 1968. Electrophysiological evidence of photoreceptors in the epistellar body of *Eledone moschata*. Nature, Lond. 220: 1332–1334.

MAURO, A., and O. STEN-KNUDSEN. 1972. Light-evoked impulses from extraocular photoreceptors in the squid *Todarodes*. Nature, Lond. 237: 342–343.

MESSENGER, J. B. 1967. Parolfactory vesicles as photoreceptors in a deep-sea squid. Nature, Lond. 213: 836–838.

NICOL, J. A. C. 1967. The luminescence of fishes. Symp. Zool. Soc. Lond. 19: 27–55.

NISHIOKA, R. S., I. R. HAGADORN and H. A. BERN. 1962. The ultrastructure of the epistellar body of the octopus. Z. Zellforsch. 27: 406–421.

NISHIOKA, R. S., I. YASUMASU, A. PACKARD, H. A. BERN, and J. Z. YOUNG. 1966. Nature of vesicles associated with the nervous system of cephalopods. Z. Zellforsch. 75: 301–316.

PÜTTER, A. 1902. Die Augen der Wassersäugethiere. Zool. Jber. 2, 17: 99.

YOUNG, J. Z. 1929. Sopra un nuovo organo dei cephalopodi. Boll. Soc. Ital. Biol. Sper. 4: 1,022–1,024.